ON THE VALIDITY OF THE THEROCEPHALIAN FAMILY LYCOSUCHIDAE (REPTILIA, THERAPSIDA)

By

J. A. VAN DEN HEEVER

South African Museum, Cape Town

(With 9 figures)

[*MS. accepted 29 November 1979*]

ABSTRACT

The taxonomic position of the therocephalian family Lycosuchidae is discussed in the light of published accounts and a re-examination of most of the type material, together with additional information from undescribed specimens of early therocephalians. It is shown that the primary distinguishing characteristic of the Lycosuchidae which separates it from the Pristerognathidae, i.e. two simultaneously functional canines in each maxilla, is based on a misinterpretation. It is therefore concluded that the family consists of an unnatural grouping of members of the Pristerognathidae and should consequently be regarded as invalid.

CONTENTS

INTRODUCTION

The early Therocephalia of the upper Permian Tapinocephalus Zone (Dinocephalian and Pristerognathus/Diictodon Assemblage Zones of Keyser & Smith 1979) of the Beaufort Series of the South African Karoo are generally poorly understood in comparison with other therapsid groups such as the Dicynodontia and the Cynodontia, mainly as a result of the intractable matrix in which the material is usually found. Since the dentition of an unprepared specimen is often its most distinctive feature the number and position of the teeth have been predominantly used in the past to distinguish between the various taxa of the group. Consequently, serious doubts have only recently been raised about the naturalness of taxa which have existed in the literature, e.g. the Lycosuchidae (Haughton & Brink 1955). Since the family Lycosuchidae was established its relatively rare members, identified principally by the possession of two maxillary canines, have always been regarded as closely allied to

Ann. S. Afr. Mus. **81** (2), 1980: 111–125, 9 figs.

the more abundant family Pristerognathidae, contemporary therocephalians with one maxillary canine. Most authors (Haughton & Brink 1955; Kermack 1956; Romer 1956; Watson & Romer 1956; Boonstra 1969) who have discussed the early Therocephalia have placed great taxonomic weight on the number of canines and consequently the concept of double-canined therocephalians is widespread in the literature. Illustrations of early therocephalians usually present the double-canined *Lycosuchus* as a general representative of the group (Du Toit 1954; Romer 1956, 1966).

Kermack (1956) demonstrated in the Therocephalia and the Gorgonopsia the existence of two upper canine positions which alternate in housing a single functional canine. According to Hopson (1964) this is also the case in the cynodont *Thrinaxodon liorhinus* and probably most other cynodonts as well. From this it is to be expected that while the functional canine was being replaced, the animal would have two canines of different ages in each maxilla, superficially similar to the condition frequently observed in living mammals when the permanent canine is in the process of replacing the milk canine (Fig. 1). Kermack also described a lycosuchid *Trochosaurus major* with two erupted canines and states that the possession of two simultaneously functional canines was primitive for Therocephalia. This idea probably stems from the view that a similar condition was thought to typify sphenacodont pelycosaurs, the presumed ancestors of therapsids.

In an important paper Mendrez (1972) established the existence of an incipient *crista choanalis* in the pristerognathids *Pristerognathus polyodon* and *Ptomalestes avidus*, situated on the inner surface of the maxilla medial to the canines. She interpreted this structure as the first step on the way to the development of a bony secondary palate as in mammals. Since the gorgonopsian maxilla is completely smooth in this area (Kemp 1969), this structure makes it possible to distinguish readily between the otherwise very similar snout fragments or isolated maxillae of therocephalians and gorgonopsians. Mendrez

Fig. 1. Stereophotograph of the left maxilla of *Felis caracal* (SAM–ZM38191) to show the eruption of the permanent canine anterolingual to the milk canine. Scale = 10 mm.

(1972) also noted the presence of two canine positions in pristerognathids (but did not cite Kermack's prior discovery of this fact) and states at page 2961: '*Pristerognatus polyodon* ainsi que *Ptomalestes avidus* possèdent également une autere caractéristique qui, selon les descriptions classiques, était, parmi les Pristerosauria de la zone à *Tapinocephalus*, la propriété exclusive des Lycosuchidae, à savoir la présence de deux canines de chaque côté de la tête. Ceci diminue le nombre déjà faible des caractères opposant ces deux familles. Il est fort probable que le Pristerognathidae décrits comme présentant un diastème entre la canine et les postcanines possédaient à cette place une seconde canine.' From this she concluded that the Pristerognathidae and the Lycosuchidae probably form a single family. However, from her statement it appears as if the Pristerognathidae possessed, like the Lycosuchidae, two functional canines in each maxilla and thus that the accepted definition of the Lycosuchidae should include the Pristerognathidae as well.

In summary, the only distinguishing characteristic of the family Lycosuchidae that at present still appears to separate it from the Pristerognathidae is the presence of two functional canines in each maxilla. In an effort to determine the validity of this morphological distinction, and thus of the family Lycosuchidae, a detailed study of the mode of replacement of the upper canines was undertaken. This study is intended to resolve the question of whether the two canines were fully mature and remained simultaneously functional for a long period of time (as assumed by most authors), or whether the condition represents a short-lived phenomenon in the replacement process, representing a stage during which the new canine is well erupted but the old functional canine has not yet been shed. The latter interpretation implies that the double-canined condition is a short segment of the normal replacing cycle of all early therocephalians and that there is no valid basis for taxonomically separating the double-canined forms (Lycosuchidae) from the Pristerognathidae.

HISTORICAL REVIEW

The first early therocephalian possessing two maxillary canines was described by Broom (1903*a*) as *Lycosuchus vanderrieti* (Figs 2–3). According to Broom the only other theriodont known at that time which possessed two canines in each maxilla was the Albany Museum specimen of the cynodont *? Cynognathus leptorhinus* Seeley (currently placed in *Cynognathus crateronotus*). However, in an addendum to the description of *Lycosuchus vanderrieti*, Broom (1903*a*) notes that *? Cynognathus leptorhinus* is similar to *Cynognathus platyceps* and that the other known species of *Cynognathus* all had only one canine; therefore, the double-canined condition in this specimen was regarded by him as temporary. Broom also drew attention to the type of *Trirachodon kannemeyeri* Seeley which on one side of the snout, in front of the canine, shows the tip of a second canine similar to that in both *Cynognathus* and *Lycosuchus*. Broom (1903*a*) felt that the anterior canine in all these genera is the morphological equivalent of the permanent mammalian canine and the

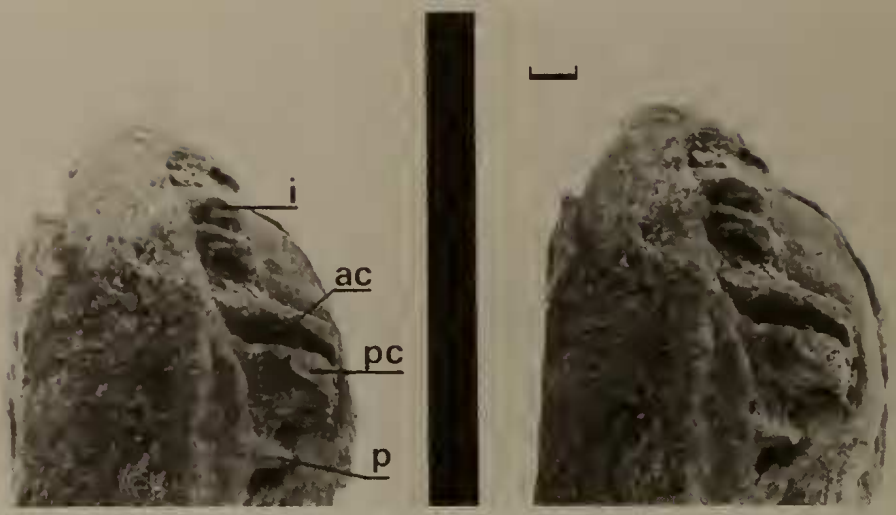

Fig. 2. Stereophotograph of the right maxilla of the type skull of *Lycosuchus vanderrieti* (Stellenbosch D173) to show the canines. The specimen is covered with polymethylmethacrylate for preparation in acid. Scale = 10 mm.

Fig. 3. Stereophotograph of the left maxilla of the type skull of *Lycosuchus vanderrieti* to show the canines. The specimen is covered with polymethylmethacrylate for preparation in acid. Scale = 10mm.

posterior canine is the equivalent of the deciduous canine of mammals. He also stated that both teeth may, however, have been functional for some time in *Lycosuchus* and the higher theriodonts because the posterior canine which developed first is more powerful and the anterior canine is 'peculiarly specialized' as if developed for a different function. The suggestion of separate functions was due to his observation that both the anterior and the posterior borders of the anterior tooth are serrated, whereas only the posterior border of the posterior tooth appeared to be serrated.

Fig. 4. Stereo photograph of the left maxilla of the type specimen *Trochosuchus acutus* (SAM–1076) to show the canines. Scale = 10mm.

Broom (1903*b*) described the isolated maxilla of a second therocephalian possessing two canines as *Lycosuchus mackayi*. Not until five years later (Broom 1908), however, when describing the double-canined *Hyaenasuchus whaitsi*, does he mention the fact that he now regards both canines in these early therocephalians as being *simultaneously* functional with neither of them being a replacement tooth. In the same article Broom described the anterior part of a small therocephalian skull as *Trochosuchus acutus*, noting the presence of two maxillary canines, the anterior being the smaller (Fig. 4).

Broom (1915) described *Trochosuchus major* specifically, stating that neither of the two canines in the maxilla is a replacement tooth and that in the light of the descriptions of *Lycosuchus*, *Hyaenasuchus* and *Trochosuchus* he regards these genera as having two large canines functioning simultaneously in each maxilla.

Haughton (1915) in his description of *Trochosaurus intermedius* followed Broom in interpreting the two canines present in each maxilla as being simultaneously functional, notwithstanding the fact that they differed in size and that a replacement tooth was situated medial to the anterior canine in each maxilla.

In his book on the mammal-like reptiles of South Africa, Broom (1932) redescribed all of the species with two canines in each maxilla and stated that both teeth are simultaneously functional because more than a dozen specimens were then known to possess this arrangement of teeth. He regarded them as a

group separate from the Pristerognathidae but did not formally establish a new family for them. (*Lycosaurus mackayi* at his p. 50 is an error and should read *Lycosuchus mackayi*.) He also synonymized *Trochosaurus intermedius* (Haughton, 1915) with *Trochosuchus major* (Broom, 1915) under the name *Trochosaurus major*. He retained the genus *Trochosuchus* for the single specimen of *Trochosuchus acutus* (Broom, 1908).

A third specimen of *Trochosaurus major* was described by Boonstra (1934) who indicated in the text as well as in the figures that the canines were undergoing replacement. He also noted the relatively broad epipterygoid which is narrowest in the middle and expanded dorsally and ventrally.

Broom (1936*a*) described *Trochorhinus vanhoepeni* as closely allied to *Trochosaurus major* and possessing two canines of unequal size, the larger being anterior.

Broom (1936*b*) described *Trochosaurus dirus* as having two large functional canines in each maxilla. However, the canines are at different stages of development and the roots of their eventual replacements are visible medially. He notes that both canines are functional and situated so close together that they probably functioned as one tooth. Furthermore he states that: '. . . each anterior canine has a very young replacing tooth; but the posterior canine on the left is being replaced by an already well-developed successor. On the right side the specimen is imperfect but the inner canine is of large size and apparently functional. Probably the outer canine is shed or being absorbed.'

No new early therocephalian specimens showing double upper canines were described after 1936. Romer (1945) included all of the above-mentioned genera in the Pristerognathidae.

Although Broom (1932) developed the rather loose concept of double-canined therocephalians, it was actually Houghton & Brink (1955) who established the family Lycosuchidae, for which they gave the following diagnosis: 'Medium-sized therocephalians with two large functional canines in each maxilla.' They listed the species as: *Hyaenasuchus whaitsi* Broom, 1908; *Lycosuchus vanderrieti* Broom, 1903 (not 1902 as given by Haughton & Brink); *Lycosuchus mackayi* Broom, 1903; *Trochorhinus vanhoepeni* Broom, 1936; *Trochosaurus major* (Broom, 1915), and *Trochosaurus dirus* Broom, 1936. The single specimen of *Trochosuchus acutus* was referred by them to the family Akidnognathidae. Tatarinov (1974) ascribes the establishment of the family Lycosuchidae to Haughton (1924). The references in Tatarinov's article reveal that the paper in question was actually published in 1925; however, in this paper Haughton retained the double-canined forms in the family Pristerognathidae.

Shortly thereafter, Watson & Romer (1956) followed Romer (1956) who independently established the family Trochosuchidae comprising the same genera as those placed by Haughton & Brink (1955) in the Lycosuchidae. They also synonymized *Trochosaurus* Haughton, 1915, with *Trochosuchus* Broom, 1908. Watson & Romer (1956) diagnosed the family Trochosuchidae as: 'Large

therocephalians which resemble the Pristerognathidae in fundamental features of their structure but differ in having a much lower skull with a broad and rather flattened snout, a sagittal crest never elevated and the occiput transversely widened. They may have six incisors and normally two canines, each separately replaced.' Since their classification is predated by that of Haughton & Brink (1955) the name Lycosuchidae has precedence and has been used by nearly all subsequent authors, e.g. Boonstra (1969, 1971, 1972), Mendrez (1972), and Tatarinov (1974); Lehman (1961: 232), however, incorrectly follows Watson & Romer (1956). Von Huene (1956) retains the members of the Lycosuchidae within the Pristerognathidae.

In spite of having synonymized *Trochosaurus* with *Trochosuchus* (Watson & Romer 1956), Romer (1966), synonymized the Lycosuchidae of Haughton & Brink (1955) with a new family, the Trochosauridae. This was apparently done to facilitate the inclusion of *Trochosuchus* in another family, the Alopecodontidae (Romer 1966). However, Haughton & Brink (1955) had placed *Trochosuchus* in the Akidnognathidae (defined as having one small canine in front of the large functional canine) a family not recognized by Romer (1966), and they described the Alopecodontidae as therocephalians with two small canines in front of the large functional canine in the maxilla. The weathered type specimen of *Trochosuchus acutus* (SAM–1076) in the South African Museum has one canine in the right maxilla and two canines in the left maxilla, the anterior being the smaller (Fig. 4). However, the last incisor appears to lie within the maxilla when viewed laterally and may have been mistaken for a small canine by Romer.

The genera included by Watson & Romer (1956) in the Trochosuchidae (Lycosuchidae) do not have larger skulls than those early therocephalians possessing a single maxillary canine, and an examination of the available material indicates that the other diagnostic differences of the family can be attributed to post-mortem distortion. Consequently, in a later description of the Lycosuchidae, Boonstra (1969) characterizes the family as: 'Early fairly large Therocephalia with fairly broad flattened skulls with two functional canines in the maxilla, advanced broadened epipterygoid and low sagittal crest. Otherwise very similar to pristerognathids. With four monotypic genera.' However, as Mendrez (1972) quite rightly points out, the so-called broad epipterygoid of the Lycosuchidae is actually known in one specimen only, *Trochosaurus major* (BMNH R5747), and it is, in fact, no broader than that of the pristerognathid *Ptomalestes avidus*.

MATERIAL AND TECHNIQUES

The type material of *Tapinocephalus* Zone therocephalians at the South African Museum was examined. In addition a complete therocephalian skull (G.S. C60) with lower jaw, lacking only the occipital bones, was borrowed from the Geological Survey. The medial aspect of the right maxilla of this specimen was carefully prepared by mechanical means to show the canines.

The type skull of *Lycosuchus vanderrieti* (D173), on loan from the University of Stellenbosch, is currently being prepared in an 11 per cent solution of formic acid owing to the extreme hardness of the matrix. It is at present still covered with polymethylmethacrylate (Figs 2–3), but the double canines are well preserved and have been examined.

Other material was prepared mechanically where necessary. In addition, the right maxilla of an unidentified species of therocephalian, SAM–K317 (identified as therocephalian according to the method of Mendrez (1972)), was sectioned frontally on a Beuhler Isomet Low Speed Saw at intervals of 2 mm. One section was stained with Alizarin Red S in a 4 per cent solution of potassium hydroxide to show the resorption of the canine root.

All photographs were taken on Kodak Panatomic-X film with a stereo apparatus built by N. J. Eden of the South African Museum.

DESCRIPTION AND DISCUSSION

The inner surface of the left maxilla of therocephalian SAM–K317 shows a distinct canine boss which contains the two canine alveoli (Fig. 5). The relative positions of the roots are visible as two smaller bulges separated by a shallow vertical sulcus. This condition can also be seen in the type of the pristerognathid *Ptomalestes avidus*, SAM–11942. The functional canine lies in the anterior alveolus and is broken off at the alveolar border. No tooth is externally visible in the posterior alveolus. The right maxilla of SAM–K317 shows the same features as does the left side, but a frontal section through the posterior alveolus shows the root of an old canine being resorbed from the alveolar border upwards (Figs 5–6).

The skull of Geological Survey specimen C60 has been compressed laterally, but in lingual view the maxilla clearly shows the canine boss with the functional canine in the anterior alveolus (Fig. 7). A replacement canine of which the tip is serrated both anteriorly and posteriorly is erupting from the posterior alveolus. This condition is identical to that in the left maxilla of *Lycosuchus*

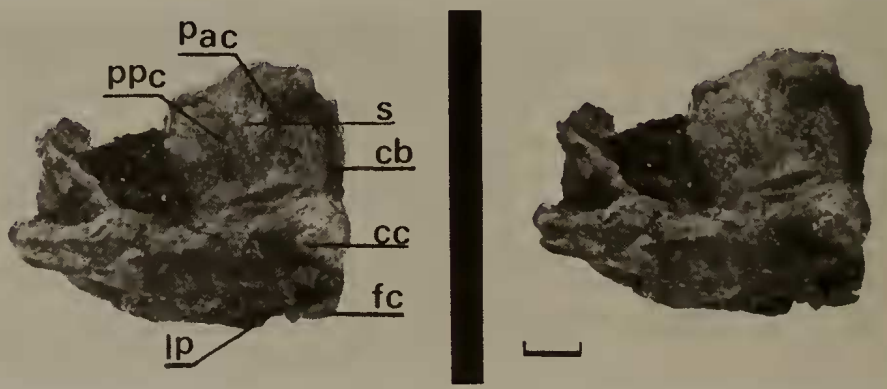

Fig. 5. Stereophotograph of the medial surface of the left maxilla of an unidentified pristerognathid (SAM–K317) showing the boss containing the canine alveoli. Anterior is to the right. Scale = 10 mm.

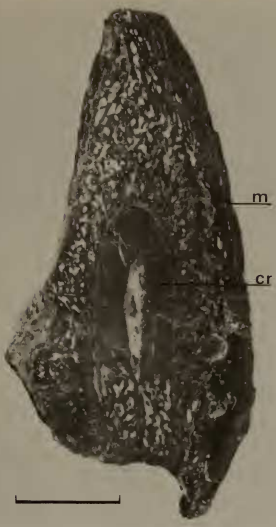

Fig. 6. Frontal section through the posterior canine alveolus of the right maxilla of an unidentified pristerognathid (SAM–K317) to show the resorption of the old canine root and its replacement by spongy bone.
Scale = 10 mm.

vanderrieti except that in the latter the younger tooth lies in the anterior position (Fig. 3).

See externally only, G.S. C60 would have to be classified as a lycosuchid according to the accepted definition of the family. However, the diameter of the posterior alveolus is the same as that of the anterior and much larger than that of the erupting canine. This suggests that the posterior alveolus was probably occupied previously by a large canine and that the immature tooth is not the first to have erupted in that position. Medial to the functional canine (Figs 7–8) an unerupted replacement canine is visible where the bone of the

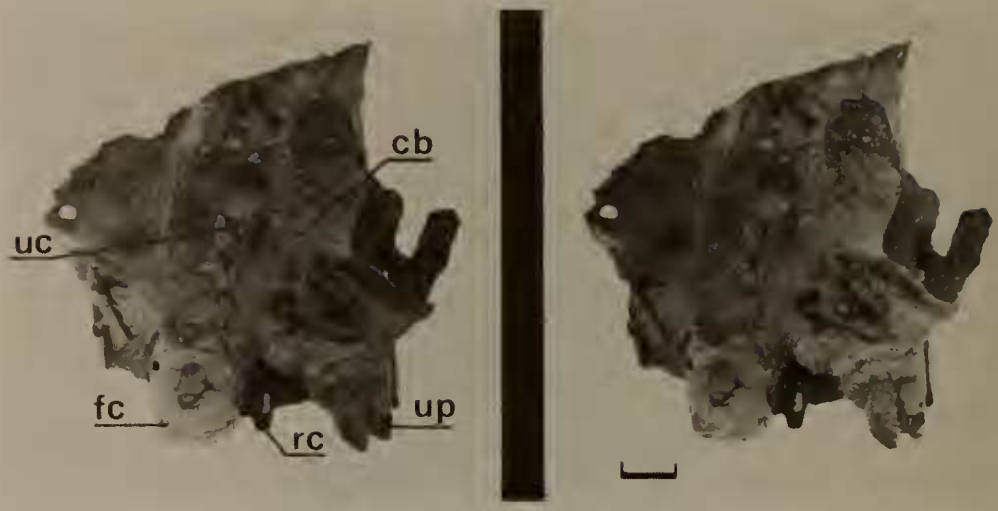

Fig. 7. Stereophotographs of the medial surface of the right maxilla of an unidentified pristerognathid (G.S. C60) showing the boss containing the canine alveoli and the sequence of canine replacement. Scale = 10 mm.

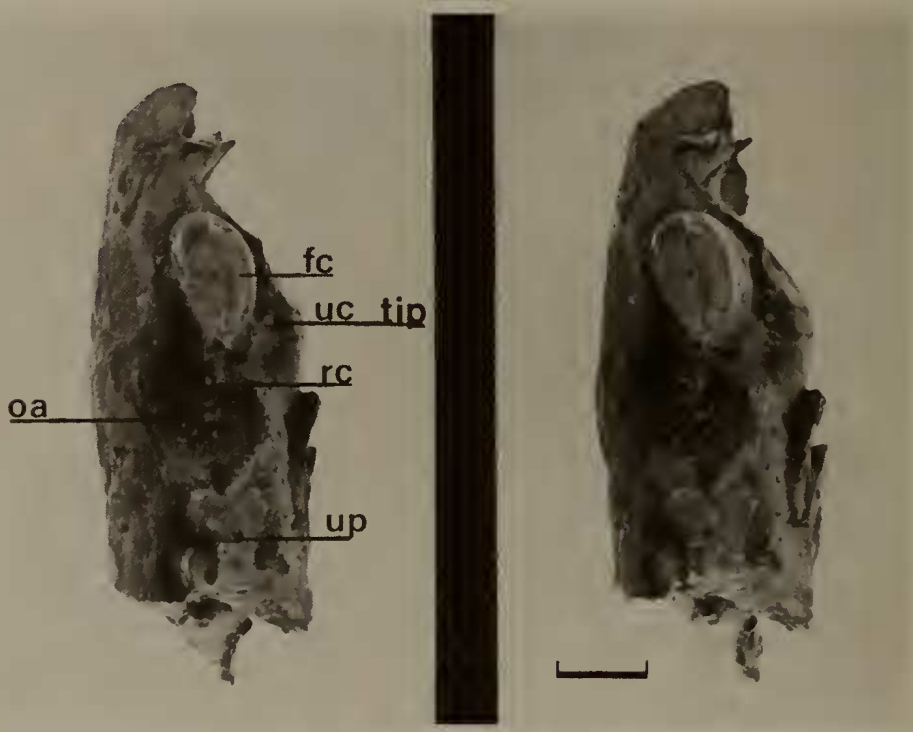

Fig. 8. Stereophotographs of a ventral view of the right maxilla of an unidentified pristerognathid (G.S. C60) to show the sequence of canine replacement. Scale = 10 mm.

medial wall is damaged. In this 'lycosuchid', then, there is direct evidence that the sequence of canine eruption alternates between the two alveoli in such a way that the time lapse between the eruption of teeth in the two alveoli produces a single functional canine at a time. This is also the most likely interpretation of the condition in the type of *Lycosuchus vanderrieti*. Specimens with two large canines in the same maxilla represent the terminal stages of the older tooth of the pair.

Since the second canine is older than the first in *Lycosuchus vanderrieti*, it would naturally be more powerful than the immature tooth, and since both tips of the posterior canines in *Lycosuchus* are damaged, Broom (1932) had no grounds for stating that the anterior canines are 'peculiarly specialized' for a different function. In fact, specimens of therocephalians which have complete canines show serrations at the tips of these teeth both in front and behind, regardless of whether the tooth is in the anterior or posterior position.

Kermack (1956) regards the single lycosuchid specimen (*Trochosaurus major*, BMNH R5747) described in his paper as one of the most primitive of the therocephalians because it has two functional canines in each maxilla (Fig. 9). By his own description (Kermack 1956: 114) the roots of replacement canines can be seen in a fracture lying lingual to each of the canines in the right maxilla. The anterior of this pair is in a more advanced stage of development than the posterior, which strongly suggests that the two large functional teeth are also of different ages. On the left, the fracture is such that the replacement teeth cannot be seen but the large canines are clearly also of differing ages since the anterior canine was still in the process of erupting and has a wide-open pulp cavity. This indicates not that both teeth were functional at the same time but rather that replacement was taking place at the time of death. However, Kermack (1956: 115) states: 'This specimen compares closely with the two specimens of *Aelurosaurus* (R339 and R855a). The only essential difference is that, in the two gorgonopsids the pair of alveoli in the maxilla each alternately bears the functional canine, while in the therocephalian each bears a functional tooth simultaneously. The difference is one of timing only.'

Kermack (1956: 121) notes further that in sphenacodont pelycosaurs such as *Dimetrodon*, as well as in *Trochosaurus*, two functional canines were present in each maxilla and elsewhere (Kermack 1956: 130) he states: 'As in *Dimetrodon* there was a pair of functional upper canines on each side in these primitive therocephalia, and they were replaced alternately. The functional replacement for each of the pair was the next number of its own tooth family. Like *Dimetrodon* when one of the upper canines was being replaced, these Therocephalia must have had but one functional canine on that side of the jaw.'

Kermack (1956) apparently implies here that in *Dimetrodon* and *Trochosaurus*-like primitive therocephalians the double canine condition was the prevailing one, whilst the period during which only one canine was functional was, in fact, of a comparatively short duration, i.e. there were normally two upper canines functioning simultaneously.

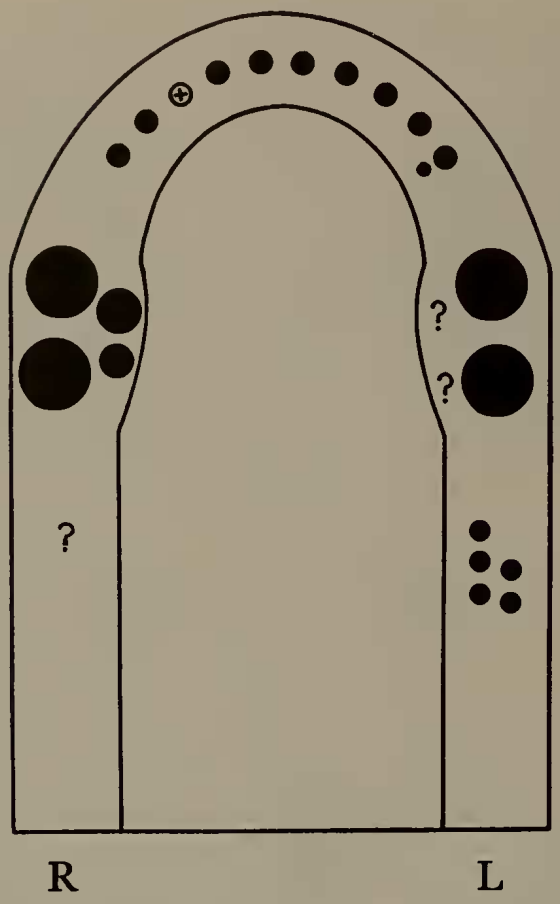

Fig. 9. Diagram from Kermack (1956) to show the canines and canine replacements of *Trochosaurus major* (BMNH R5747).
R = right, L = left.

The South African Museum holds at least 112 specimens of early therocephalian skulls and skull fragments in which the canines can be seen. Of these, fourteen specimens possess two canines in either one or both of the maxillae, including the above-mentioned types. This ratio of roughly one specimen with double canines for every seven with a single canine per maxilla illustrates the relative scarcity of the two-canine condition and indicates that the period during which two canines were externally visible was probably of relatively short duration. In no South African Museum specimen with double canines are there any indications that the teeth are of the same age and, from the literature cited above, it is also clear that in *all* described specimens of Lycosuchidae the canines are also staggered in age. It is highly improbable that in carnivores such as the Therocephalia, in which the tips of the canines are serrated both anteriorly and posteriorly, these teeth would have functioned optimally as a closely packed unit. Not only would the efficiency of penetration be impaired

by the bulky 'unit' compsed of two large teeth, but also, since some of the serrations would be obscured, the teeth would tear less efficiently as well. Therefore, it seems more likely that these animals possessed a single piercing canine of long functional duration and that the period of replacement, during which two canines were externally visible in each maxilla, was as short as possible. This is indicated by the relatively few specimens actually showing this condition. The *functional* replacement for each canine would then not be the next tooth of its own family (i.e. in the same tooth position), but the next tooth erupting from the other canine alveolus. This model of canine tooth replacement is supported by the work of Edmund (1960) who, contrary to the observation of Kermack (1956), found that in *Dimetrodon* the pair of canines in each maxilla were only occasionally functional at the same time and usually alternated so that only one tooth was functional at a time.

CONCLUSIONS

Kermack (1956) is correct in stating that in the Therocephalia the two canine alveoli each bore the functional canine alternately, but he is incorrect in assuming that in the Lycosuchidae, e.g. *Trochosaurus*, both alveoli normally bore functional canines simultaneously. In view of the importance of canines in carnivore dentitions it is to be expected that the replacement of any fang will develop at such a time and replace the mature canine in such a way that the animal is never without at least one functional canine in each maxilla. This necessitates a period of time when the erupting replacement coexists with the old functional tooth. Because of the distinct advantages of the single over the double functional canine condition, the actual period of time in which the two canines were externally visible was probably kept as short as possible.

The Lycosuchidae is therefore not a separate primitive therocephalian family but consists of members of the Pristerognathidae in which death occurred while the erupting replacing canine was visible externally. *Lycosuchus vanderrieti* (Figs 2–3) is an especially good example of this condition. Therefore the family Lycosuchidae (=Trochosauridae) represents an unnatural grouping of members of the Pristerognathidae, and it is suggested here that it be invalidated.

ACKNOWLEDGEMENTS

I wish to thank the following persons: Mrs K. Rial and Mr N. J. Eden, both of the Department of Palaeontology at the South African Museum for, respectively, preparation and photography, Professor W. J. Verwoerd of the Department of Geology at the University of Stellenbosch, and Dr A. W. Keyser of the Geological Survey in Pretoria for the loan of specimens, Dr J. A. Hopson of the University of Chicago for critically reading the manuscript, and Mrs P. Eedes and Mrs G. E. Blaeske, of the South African Museum, for typing.

REFERENCES

Boonstra, L. D. 1934. A contribution to the morphology of the mammal-like reptiles of the suborder Therocephalia. *Ann. S. Afr. Mus.* **31**: 215–267.

Boonstra, L. D. 1969. The fauna of the *Tapinocephalus* zone (Beaufort beds of the Karoo). *Ann. S. Afr. Mus.* **56**: 1–73.

Boonstra, L. D. 1971. The early therapsids. *Ann. S. Afr. Mus.* **59**: 17–46.

Boonstra, L. D. 1972. Discard the names Theriodontia and Anomodontia: a new classification of the Therapsida. *Ann. S. Afr. Mus.* **59**: 315–338.

Broom, R. 1903*a*. On an almost perfect skull of a new primitive theriodont (*Lycosuchus vanderrieti*). *Trans. S. Afr. phil. Soc.* **14**: 197–205.

Broom, R. 1903*b*. On some new primitive theriodonts in the South African Museum. *Ann. S. Afr. Mus.* **4**: 147–156.

Broom, R. 1908. On some new therocephalian reptiles. *Ann. S. Afr. Mus.* **4**: 361–367.

Broom, R. 1915. Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History. II. Permian, Triassic and Jurassic reptiles of South Africa. *Bull. Am. Mus. nat. Hist.* **25**: 105–164.

Broom, R. 1932. *The mammal-like reptiles of South Africa and the origin of mammals*. London: Witherby.

Broom, R. 1936*a*. On some new genera and species of Karroo fossil reptiles, with notes on some others. *Ann. Transv. Mus.* **18**: 349–386.

Broom, R. 1936*b*. On the structure of the skull in the mammal-like reptiles of the suborder Therocephalia. *Phil Trans. R. Soc.* **226**: 1–42.

Du Toit, A. L. 1954. *The geology of South Africa*. 3rd ed. S. H. Haughton *ed.* Edinburgh; London: Oliver & Boyd.

Edmund, A. G. 1960. Tooth replacement phenomena in the lower vertebrates. *Life Sci. Contr. R. Ont. Mus.* **52**: 1–190.

Haughton, S. H. 1915. On two new therocephalians from the Gouph. *Ann. S. Afr. Mus.* **12**: 55–57.

Haughton, S. H. 1925. A bibliographical list of pre-Stormberg Karroo Reptilia, with a table of horizons. *Trans. R. Soc. S. Afr.* **12**: 51–104.

Haughton, S. H. & Brink, A. S. 1955. A bibliographical list of Reptilia from the Karroo beds of Africa. *Palaeont. afr.* **2**: 1–187.

Hopson, J. A. 1964. Tooth replacement in cynodont, dicynodont and therodephalian reptiles. *Proc. zool. Soc. Lond.* **142**: 625–654.

Kemp, T. S. 1969. On the functional morphology of the gorgonopsid skull. *Phil. Trans. R. Soc.* (B) **256**: 1–83.

Keyser, A. W. & Smith, R. M. H. 1979. Vertebrate biozonation of the Beaufort Group with special reference to the western Karoo basin. *Ann. geol. Surv. Pretoria* **12**: 1–35.

Kermack, K. A. 1956. Tooth replacement in mammal-like reptiles of the suborders Gorgonopsia and Therocephalia. *Phil. Trans. R. Soc.* (B) **240**: 95–133.

Lehman, J. P. 1961. Therocephalia. *In: Traite de Paleontologie* **6**: 224–245. J. Piveteau, ed.

Mendrez, C. 1972. Premières ébauches d'un palais secondaire osseux chez les reptiles mammaliens. *C. r. Acad. Sci. Paris* **274**: 2960–2961.

Romer, A. S. 1945. *Vertebrate paleontology*. 2nd ed. Chicago: University of Chicago Press.

Romer, A. S. 1956. *The osteology of the reptiles*. 1st ed. Chicago: University of Chicago Press.

Romer, A. S. 1966. *Vertebrate paleontology*. 3rd ed. Chicago: University of Chicago Press.

Tatarinov, L. P. 1974. *Theriodonts of the USSR*. Moscow: NAUCA.

Von Heune, F. 1956. *Paläontologie und Phylogenie der niederen Tetrapoden*. Jena: VEB, Gustav Fischer Verlag.

Watson, D. M. S. & Romer, A. S. 1956. A classification of therapsid reptiles. *Bull. Mus. comp. Zool. Harv.* **114**: 37–89.

ABBREVIATIONS

a.c.	anterior canine
c.b.	canine boss
c.c.	crista choanalis
c.r.	canine root
f.c.	functional canine
i.	incisor
l.p.	lower postcanine
m.	maxilla
m.c.	milk canine
o.a.	old alveolus
p.	postcanine
p.a.c.	position of anterior canine
p.ç.	posterior canine
p.ca.	permanent canine
p.p.c.	position of posterior canine
r.c.	replacing canine
s.	sulcus
u.c.	unerupted canine
u.c. tip	tip of unerupted canine
u.p.	upper postcanines
BMNH	British Museum of Natural History
G.S.	Geological Survey, Pretoria
SAM	South African Museum.